Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel

Citation for published version:
Jones, HEM, White, A, Geddes, N, Clavey, P, Farries, J, Dearnley, T, Boots, M & Lurz, PW 2016, 'Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel', *Hystrix, the Italian Journal of Mammalogy*, vol. 27, no. 1. https://doi.org/10.4404/hystrix-27.1-11673

Digital Object Identifier (DOI):
10.4404/hystrix-27.1-11673

Link:
Link to publication record in Heriot-Watt Research Portal

Document Version:
Peer reviewed version

Published In:
Hystrix, the Italian Journal of Mammalogy

Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel

Jones, H.E., White, A., Geddes, N., Clavey, P., Farries, J., Dearnley, T., Boots, M. and Lurz, P.W.W.

Corresponding Author: Dr Peter Lurz

Corresponding Author Address: Lurzengasse 3, D-97236 Randersacker, Germany

Corresponding Author e-mail: lurzpww@gmail.com

Authors

JONES, HANNAH, E.
Department of Mathematics and the Maxwell Institute for Mathematical Sciences, Heriot-Watt University, Edinburgh, EH14 4AS.

WHITE, ANDREW
Department of Mathematics and the Maxwell Institute for Mathematical Sciences, Heriot-Watt University, Edinburgh, EH14 4AS.

GEDDES, NEVILLE
Forestry Commission, North England Forest District, Eals Burn, Bellingham Northumberland, NE48 2HP, UK

CLAVEY, PAUL
Forestry Commission, North England Forest District, Eals Burn, Bellingham Northumberland, NE48 2HP, UK

FARRIES, JONATHAN
Forestry Commission, Church House, Church Street, Rothbury, Morpeth, Northumberland, NE65 7UP, UK

DEARNLEY, TOM
Forestry Commission, North England Forest District, Eals Burn, Bellingham Northumberland, NE48 2HP, UK

BOOTS, MIKE
Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Treliever Road, Penryn, Cornwall, TR10 9EZ.

LURZ, PETER, W.W.
Lurzengasse 3, D-97236 Randersacker, Germany

Abstract

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the UK from the introduced North American grey squirrel. National measures to save the species include large conifer forest reserves where management encompasses measures to bolster the native species. However, forests are multi-purpose environments and foresters have to balance different timber production, amenity and conservation objectives. We present a mathematical modelling framework that examines the impacts of potential felling and restocking plans for two reserves, Kidland and Uswayford forests, in northern England. In collaboration with forest managers, we employed an iterative process that used the model to assess four forest design plans (felling and restocking scenarios) with the aim of improving red squirrel population viability. Overall, the model predicted that extinction in both forests at the same time was rare, but high in Uswayford (84%) alone. Survival could be drastically increased (from 16 - 70%) by felling and restocking adjustments, and improving dispersal between the two adjacent forests. This study provides an exemplar of how modelling can have a direct input to land management to help managers objectively balance the differing pressures of multipurpose forestry.

Keywords: Conservation, SEPM, population dynamics, forestry, Sciurus vulgaris

Running Head: Modelling the impact of forest design plans

Introduction

The management of forest systems will face a range of challenges in the coming decades as a result of global climate change, emerging tree diseases and a need to integrate forest ecosystem services such as timber extraction or amenity with efforts to preserve biodiversity (Bengtsson et al., 2000; Brown and Webber, 2008; Ray, 2008; Ray et al., 2010; DEFRA 2011; Shuttleworth et al., 2012). Mathematical modelling can play an important role in helping to address these challenges. In particular models that are combined with digital landcover data and knowledge of species habitat requirements and behaviour form powerful and highly successful tools for species conservation and management. Examples of modelling approaches that combine mathematical models and spatial data include GIS-based landcover mapping approaches linked with simple models to predict future land development impacts on deer (*Odocoileus hemionus*; Kline et al. 2010); using spatially explicit population models to assess the potential success of species translocations for butterflies (*Maniola jurtina*, Heikkinen et al. 2015); the development of a spatially explicit agent-based model to simulate tiger (*Panthera tigris*) population and territory dynamics (Carter et al. 2015); or the use of spatial, stochastic models to study the impact of disease-mediated competition by the introduced North American grey squirrels (*Sciurus carolinensis*) on Eurasian red squirrels (*S. vulgaris*; White et al. 2014).

A key benefit of models is their ability to pose "what if" questions that assess the likely effects of future land use changes or species management. Their use allows objective assessments of different management options and can assist in developing the most effective conservation strategies. Here we present the application of a spatially explicit, stochastic population dynamics model that was used to evaluate the likely impacts of different forest design scenarios on the population persistence of Eurasian red squirrels, a species under threat of extinction in the UK (Gurnell et al., 2004, 2014; Lurz et al. 2005).

In close collaboration with the Forestry Commission, the government forestry organisation in the UK, we examined the future felling and restocking scenarios for Kidland and Uswayford forests (Fig. 1), two spruce-dominated, conifer woodlands in the north-east of England. The two forests are part a network of 17 English conifer-dominated "strongholds" for the endangered red squirrel, where favourable habitat and management aims to reduce the competitive and disease impacts of invading grey squirrel populations (grey squirrels carry squirrelpox virus that is lethal to red squirrels; Tompkins et al. 2003) and thus ensure long term survival of local red squirrel populations (Parrott et al. 2009; Anonymous 2012; reviewed in Bosch & Lurz 2012).

A large number of forests (38% of the UK forest area) are managed by the Forestry Commission, and the Forestry Commission is a key partner in the efforts to save red squirrels in Britain. With respect to the North of England, they manage a significant or majority proportion of the seven red squirrel reserves, all of which are forests planted in the 20th century. Whilst the forests were initially established to provide a strategic timber resource, there are now multi-purpose management objectives that balance timber production with recreation and conservation. The whole of Uswayford forest and approximately half of Kidland forest is owned and managed by the Forestry Commission. The remainder of Kidland is in the hands of a number of private owners. The two forests are composed predominantly of Sitka spruce (*Picea sitchensis*) as well as a small proportion of other conifer species. They were planted on open moorland and red squirrels colonised during the last century. They are relatively isolated and therefore the likelihood of invasion by grey squirrels is low.

Monitoring for red squirrels at Kidland forest has occurred for the last 15 years on an annual basis. The forest habitat supports low-density populations of red squirrels and is thought to be unfavourable for greys. A key determinant of red squirrel abundance in these regions is resource availability which will depend on the availability of mature seed producing trees suitable for red squirrels (which in turn varies depending on felling and restocking strategies) and seed crop abundance (which varies annually due to climate patterns, weather and phenology), (Bosch & Lurz 2012). The close association of red and grey squirrels with forest habitats and their maturity make them ideal species for assessment with models (Lurz et al. 2001, 2003, 2008). Linking mathematical models with digital landcover maps, or the highly detailed UK forest stock maps which provide information on tree species (planted as single species blocks) and age classes (planting year) at high resolutions allows accurate simulations of different forest management options.

In this study we use mathematical models and digital landcover maps to assess how red squirrel abundance would change as a result of different forest design plans. The objective was to use an iterative process where modelling that assesses red squirrel population dynamics can inform the development of further forest design plans with the aim of ensuring and improving red squirrel viability. This iterative process led to the consideration of four different forest design plans (scenarios A – D outlined in the methods sections) in which the model predicted squirrel densities as Kidland and Uswayford are felled and replanted. The model study outlines the scenarios that are most favourable for red squirrel abundance and viability and this information has been used by the Forestry Commission in the production of the proposed forest design plans for these regions.

Figure 1 here

Methods

<u>Study area</u>

Kidland and Uswayford are part of the North England Forest District, in Northumberland, England. They were planted post 1960 and are commercially managed. Kidland is 2050 ha, of which 1190 ha are managed by the Forestry Commission, the rest is owned by private landowners managed by the company

Tilhill; while Uswayford is approximately 1000 ha, all managed by the Forestry Commission. The two forests are separated by less than 1 km of open land (Fig. 1), but are relatively isolated from other forested regions and surrounded by moorland. They are dominated by conifer species such as Sitka spruce, Norway spruce (*P. abies*), Scots pine (*Pinus sylvestris*), Lodgepole pine (*P. contorta*) and larch, (*Larix spp.*; see also Fig. 1). Using Forestry Commission data, we extracted the compartments that represent Kidland and Uswayford (see blue and green regions respectively in Fig. 1c) and the privately managed Tilhill area on the western side of Kidland (see red region in Fig. 1c).

<u>Carrying capacity estimate</u>

The number of squirrels the different forest compartments can support depends on habitat type, which can be estimated using Forestry Commission stockmap data (or publicly available forest inventory records for private areas). This data provides species specific habitat and age information within each compartment which can be combined with squirrel density estimates from the literature and data from the existing 15 years of local squirrel and tree seed crop survey data (Forestry Commission pers. comm.; Table 1). It is assumed that it takes 30 years for trees to reach maturity and provide suitable, regular resources (seeds) for red squirrels. As felling plans for the adjacent, privately managed forest area were not known in detail, the land was taken to be one third felled, one third immature and one third mature, which replicates a 45 year conifer rotation cycle typical for upland conifer plantations. This also kept private forest areas neutral and allowed the project to focus on assessing the impacts of any proposed Forestry Commission design plans only, without confounding the results with changes to the structure of adjacent woodland. We determined a high and low carrying capacity to reflect good and poor seed years for each compartment using published density estimates (taken from the following references: Holm (1991); Magris (1998); Lurz et al. (1995, 1998); Bosch & Lurz (2012); White et al. (2014)). The estimated red squirrel densities per hectare for each tree species class is shown in Table 1, and Fig. 2 shows the resulting high and low carrying capacities for the forests in 2012.

Red Squirrel Density (/ha)		
Tree Species	High	Low
Ash, *Fraxinus excelsior*	0	0
Birch, *Betula* spp.	0	0
Douglas fir, *Pseudotsugo menziesii*	0.45	0.17
European larch, *Larix decidua*	0.38	0.21
Grand fir, *Abies grandis*	0	0
Hybrid larch	0.38	0.21
Japanese larch, *Larix kaempferi*	0.38	0.21
Lodgepole pine	0.4	0.04
Mixed broadleaf	1	0.62
Norway Spruce	0.58	0.25
Oak, *Quercus* spp.	1	0.62
Scots pine	0.4	0.04
Sitka spruce	0.11	0.011
Sycamore, *Acer pseudoplatanus*	0	0
Western Hemlock, *Tsuga heterophylla*	0	0
Other Conifer	0.45	0.17
Other Spruce	0.2	0.02
Mixed Conifer	0.45	0.17

Table 1: Density estimates for red squirrels in the different tree species classes present in Kidland and Uswayford forest. The data was derived from the following references: Holm (1991); Magris (1998); Lurz et al. (1995, 1998); Bosch & Lurz (2012); White et al. (2014).

Figure 2 here.

Forest Design Plans (Scenarios A-D)

The initial forest design plan (named scenario A) supplied by the Forestry Commission contains felling and species specific restocking information from 2012-2052. This was created prior to the modelling assessment and was based on commercial considerations without a focus on red squirrel conservation. The felling and restocking information in scenario A can be used to produce carrying capacity maps for each year between 2012-2052 (shown for every two years in the Supplementary Information, Figs S1 and S2). The initial model predictions using scenario A were presented to the Forestry Commission in May 2014 and led to the development of three further scenarios (B, C, D) that attempted to improve red squirrel population viability while taking into account local planting and felling constraints (e.g. restrictions due to tree diseases and wind throw risks for exposed locations). We outline these scenarios below (and see Table 2 for a summary).

Scenario B considers an alternative felling plan which extended the time before some coupes were felled in Uswayford. This aimed to prevent sustained low densities in Uswayford. To compensate, some additional felling was undertaken in Kidland. Carrying capacity maps using scenario B are shown in Figs S3 & S4.

Scenario C has a similar felling trend to scenario B in Uswayford, but has a reduced rate of felling in Kidland. In addition, the tree species mixture chosen for restocking contains tree species that support a higher density of squirrels (carrying capacity maps using scenario C are shown in Figs S5 & S6).

Scenario D follows a similar trend to scenario C but the tree species chosen for restocking are chosen based on commercial priorities rather than squirrel habitat quality. They therefore do not support such a high squirrel density as scenario C (carrying capacity maps using scenario D are shown in Figs S7 & S8).

Figure 3 shows the effect of the four different forest design scenarios on the overall carrying capacity of Kidland and Uswayford.

Figure 3 here

Scenario	Date received	Summary
A	24/2/14	Original forest design plan.
B	14/10/14	Reduced felling rate in Uswayford. Increased felling rate in Kidland.
C	17/11/14	Similar to scenario B for Uswayford. Reduced felling rate in Kidland. Restocking to provide improved squirrel habitat.
D	12/2/15	Similar to scenario C, but with commercial focused restocking

Table 2: A summary of the four different forest design plans (scenarios) produced by the Forestry Commission.

In addition to the new forest design scenarios (B-D), the Forestry Commission also provided details of a potential habitat link between the forests (see Fig. S9). In the model runs we therefore considered two possibilities: (i) squirrels cannot utilise the dispersal compartment until 2045 (30 years after planting when trees are assumed to be mature) and; (ii) squirrels can utilise the compartment in 2025 (while the trees may not be suitable habitat for red squirrels after 10 years, they would provide cover for squirrels moving between Kidland and Uswayford).

<u>Model framework and setup</u>

Previous model studies that have assessed the population dynamics of red squirrels in realistic landscapes have adapted the classical deterministic modelling approach of Tompkins et al. 2003 to consider a stochastic model framework (White et al., 2014, Macpherson et al. 2015; White et al., 2016). In the current study it is important to consider the stochastic nature of the population dynamics as population abundance can reach low levels, which could result in regional population extinction. We therefore follow a similar approach to White et al. (2014) in this study. Within each forest compartment the population density of red squirrels, N, at time t, in years, is represented by the following underlying deterministic model.

$$\frac{dN}{dt} = aN\left(1-\frac{N}{K_1}\right) - bN\left(\frac{N}{K}\right) \qquad \text{for} \qquad t_n \le t < t_n + 0.5 \qquad (1a)$$

$$\frac{dN}{dt} = -bN\left(\frac{N}{K}\right) \qquad \text{for} \qquad t_n + 0.5 \le t < t_{n+1} \qquad (1b)$$

Here, we assume birth and death are density dependent and that birth only occurs for a 6 month breeding season (representing 2 litter periods between May-October) whereas death can occur throughout the year. The natural mortality rate is b=0.9 yr^{-1} (Barkalow et al., 1970) and the birth rate is a=3.0 yr^{-1} (Tompkins et al., 2003). The carrying capacity, K, is determined using Forestry Commission data for each compartment (see Fig. 2 and Figs S1-S8) and the density dependent parameter that scales the birth rate, K_1 = 2.6K is calculated to ensure that the average population density over a year is equal to the carrying capacity, K.

The deterministic model is turned into an individual based stochastic model by turning the rates for births and deaths in Equation (1) into probabilities of a birth or death “event”. We also need to consider the dispersal of individuals. We assume saturation dispersal such that individuals are more likely to disperse as the local population increases (Poethke and Hovestadt, 2002). In our models we specify that individuals disperse randomly up to a distance of 1 km and therefore could move to any compartment that is within this distance. We assume the dispersal rate, m=b, so that on average squirrels are predicted to disperse to a new compartment once in their lifetime. The spatial stochastic model is therefore:

Event	Outcome	Probability
Birth (breeding season)	$N_i \rightarrow N_i + 1$	$\left[aN_i(1 - N_i/K_1)\right]/R$
Death	$N_i \rightarrow N_i - 1$	$\left[bN_i(N_i/K_i)\right]/R$
Dispersal	$N_i \rightarrow N_i - 1;\ N_j \rightarrow N_j + 1$	$\left[mN_i(N_i/K_i)^2\right]/R$

Table 3: Possible events and their outcomes in a particular compartment *i*, with dispersal occurring to compartment *j*. The rates from Equation (1) are turned into probabilities by dividing by $R = \sum[\text{rates}]$ (the sum of the terms in square brackets summed over all compartments).

We use a Gillespie algorithm (Gillespie 1977) to select each event and update the number of individuals (and therefore the probabilities) after each event. The time between each event is given by $dt = -\ln(z)/R$ where *z* is a uniform random number between 0 and 1 (which assumes the next event is an exponentially distributed random variable; Renshaw 1993).

Using scenario A, the model outlined in Table 3 was run for 100 years with the high and low carrying capacity estimates (Fig. 2) to represent a spin-up period (see also supplementary information Figs S10 & S11). In order to reflect the natural, annual variation in resources caused by good and poor seed years (e.g. Lurz 2015), the model is also run for a scenario in which 3 years of the high carrying capacity was followed by 1 year at the low carrying capacity (3 high, 1 low scenario; Fig. S12).

Following the 100 year spin up period, 50 realisations of the model were run for a further 40 years (2012 - 2052), with the carrying capacity being updated yearly depending on the felling and replanting strategy of the scenario A forest design plan. Similarly, 50 realisations of the model were run for a further 55 years (2012-2066) updating the carrying capacity yearly depending on the strategies given in scenarios B – D.

Results

The spin up period showed that in the high scenario, the red squirrel population can be supported in the long term with an average of approximately 150 squirrels (Fig. S10). In the low scenario population extinction is predicted in all model runs (commonly within 5-20 years, Fig. S11), indicating that the red squirrel population could not persist if there were only poor seed crop years. In the 3 high, 1 low scenario, the red population can be supported in the long-term (Fig. S12). This scenario also reflects the variation in annual squirrel abundance that is reported in these forest strongholds (Forestry Commission pers. comm.) with abundance peaking at around 150 squirrels after successive good years and dropping to around 35 individuals in poor years. Since the annual variation in resources is a feature of the natural system the remaining results in this study are presented for the 3 high, 1 low scenario.

<u>Scenario A</u>

The model was run from 2012-2052 using the forest design plans outlined for scenario A and following the 3 high, 1 low seed crop scenario. Complete extinction of red squirrels in both Kidland and Uswayford was observed in 2% of the realisations (Fig. 4a). However, red squirrel extinction (by 2052) was predicted in Uswayford (only) in 84% of the realisations. When an additional 20 years was simulated beyond 2052 (Fig. 4a), the red squirrel population at Kidland stabilized, as the replanted forest compartments had matured and could support additional squirrels. However, there was minimal recovery of squirrel numbers in Uswayford. The model runs indicate that Uswayford was not recolonised by squirrels dispersing from Kidland, even though suitable habitat to support squirrel populations in Uswayford was available from 2050 onwards.

Figure 4 here

In order to investigate why dispersal from the red squirrel population in Kidland (incl. privately managed Tilhill areas) did not aid the repopulation of Uswayford in the model, we examined the distribution of mature seed-bearing habitat for red squirrels under the forest design plans of Scenario A (see Fig. S13). This indicated that there was little suitable habitat in Uswayford between 2038 and 2048 which results in the high levels of population extinction. From 2050 onwards suitable habitat was available in Uswayford, but only a small fraction of this was within the 1 km dispersal distance to the populations at Kidland. Therefore, while some compartment boundaries between Uswayford and Kidland/Tilhill are within the dispersal range for squirrels, felling and replanting meant that the occurrence of mature habitat within the dispersal range was limited.

To explore whether dispersal was a critical factor in the survival or recovery of squirrel populations at Uswayford, we therefore considered an ‘idealised’ scenario, in which dispersal was allowed to any compartment, independent of its location or distance. Figure 4(b) shows that population abundance still drops to low levels between 2040-2050 due to the low carrying capacity in Uswayford. However, the improved connectivity allows the population to recover in all model realisations. Therefore, recolonisation of Uswayford is hindered by a lack of dispersal opportunities, and a better connection between Uswayford and Kidland/Tilhill would improve recovery in Uswayford following population decline (or extinction) once mature habitat becomes available again.

These interim findings were presented to the Forestry Commission in May 2014. It was clear that the planned felling and restocking under scenario A could cause a large drop in the carrying capacities, and therefore squirrel abundance, in both Kidland and Uswayford at the same time. Based on the modelling assessment, the key recommendations to reduce the likelihood of red squirrel population included:

- adjusting the forest management plans so that low carrying capacities (large areas that are felled and/or plantations of an age that do not yet produce seeds) are out of phase in each forest.

- adjusting the tree mixtures to improve the overall carrying.

Discussions with the Forestry Commission also suggested that the model system could be used to consider the effect of an improved connection between Kidland/Tilhill and Uswayford. This would allow one forest to act as a source of squirrels if temporary extinctions were to occur in the other. The impact of a habitat link between forests (see Fig. S9) was considered for scenarios B-D (see below).

Scenarios B, C and D

The scenario A model predictions suggest that Kidland could generally maintain a continuous squirrel population, while the population in Uswayford would fall to very low levels, supporting few squirrels until a slight increase by 2052 (Figs 3a and 4a). The chance of population extinction in Uswayford when realistic seed crop patterns were modelled is high (84%). Scenarios B – D were developed by the Forestry Commission in response to these model findings.

In the absence of a dispersal corridor, model simulations for Scenario B (Fig. 5a) show that red population abundance in Uswayford is predicted to fall by around 2052. However, following 2052 the habitat improves and by 2066, populations are recovering to sustainable levels. There is a 46% chance of extinction in 2052 (compared to 84% for scenario A). The scenario C forest design plan further reduced the felling rate in Kidland and model predictions for this scenario support a larger total population of squirrels throughout the period (Fig 5d). While there is still a drop in the abundance of squirrels in Uswayford in 2052, only 30% of model realisations result in extinction in Uswayford. Scenario C would therefore reduce the probability of squirrel extinction compared to both scenarios A and B. The model realisations for scenario D (Fig. 5g) are very similar to those in scenario C, with a chance of extinction in Uswayford of 30% (the same as in scenario C). The total overall population is slightly lower in scenario D than scenario C as the trees used in restocking do not support as many squirrels.

Figure 5 here

Whilst the new scenarios improve population viability for red squirrels, population abundance still drops to low levels (by around 2050) with a risk of extinction in Uswayford. Population recovery in Uswayford was improved when a dispersal link was included. Model results indicate that recovery was fastest when the dispersal corridor could be utilised 10 years after planting (Fig. 5). Populations in Uswayford (and the total population) were highest by 2066 in Scenario C (Fig. 5). To compare the four forest design scenarios (A-D) in more detail, we determined the probability of red squirrels persistence in 2052 under scenario B-D when the additional dispersal corridor between Kidland and Uswayford was included in the model. The chance of total extinction in both Kidland and Uswayford was rare and only occurred in one realisation in the 3 high, 1 low carrying capacity case in Scenario A (and in no other model runs). We therefore focus on Uswayford and determine the probability of survival in Uswayford. Without a dispersal corridor between Kidland and Uswayford, the chance of survival is low in scenario A (16%), higher in scenario B (54%) and further increased in scenarios C (70%) and D (70%) (Fig. 6). Population extinction can still occur in Uswayford when the dispersal corridor is included, but in all of these cases the model predicts improved survival in Uswayford in 2052 (Fig. 6), and that Uswayford will be re-populated by 2066 (when the corridor is included). Therefore, the dispersal corridor reduces the chance of extinction and significantly improves the re-population of Uswayford if extinction does occur.

Figure 6 here

Discussion

Managing forests to improve species conservation and diversity is increasingly important (Hansen et al., 1991; Lindenmayer et al., 1998) but can often conflict with commercial forestry interests which are influenced by economic pressures that may be detrimental to many species (Radcliffe & Petty, 1986).
Comprehensive and integrated model frameworks can be used to represent ecosystems and their services and to design appropriate methods to handle forest management impacts (Filyushkina et al., 2016). However, efforts to manage forest ecosystem services and preserve endangered species can only succeed when scientists, foresters and landowners work together. Whilst some forest species such as the Capercaillie (*Tetrao urogallus*) benefit from intact, mature old-growth forests (e.g. Mikoláš et al., 2015), the conservation efforts for red squirrels can be integrated with standard forest operations over the whole woodland area. A high degree of flexibility in red squirrel habitat and space use in conifer forests (Lurz et al., 1995, 1997, 1998, 2000) allows the species to exist at low population densities in production conifer plantations typical of British uplands. These areas offer refuges from the introduced, broadleaf-specialist grey squirrels and form the backbone of current red squirrel conservation efforts in the North of England (Pepper and Patterson, 1998; Parrott et al., 2009).
Management for red squirrels in these conifer dominated areas focuses on a few basic recommendations:

- maintaining seed food supply for red squirrels through a minimum level of tree diversity;
- considering forest age structure to ensure there are sufficient mature trees of seed bearing age to support a population;
- maintaining canopy connectivity after thinning and dispersal links within the forest to allow squirrels to resettle as a result of harvesting operations without the risk of predation on open ground (Lurz et al., 2008; Anonymous, 2012; Flaherty et al., 2012).

The permanent retention of small areas capable of supporting a population would also speed up re-colonisation of nearby woodland blocks following harvesting and replanting.

The integration of information on red squirrel population dynamics (Lurz et al., 2005) with local forest management expertise, and mathematical modelling approaches (White et al., 2014) allows assessments of potential impacts of different forest management options on red squirrel abundance. The results of the current study clearly indicate that an iterative, close collaboration can drastically reduce the likely extinction risk for red squirrel populations at Kidland and Uswayford forests and can help in the development of robust conservation strategies. Model findings showed that changes to harvesting and restocking could improve red squirrel viability by ensuring that there was sufficient suitable habitat. Furthermore, an important factor in improved population survival was the consideration of Uswayford and Kidland as one forest system, realised by the inclusion of a linking, dispersal corridor (see Fig. S9). Given differences in respective forest ages, and a necessity for timber extraction due to high wind-throw risks and contractual obligations, the management of the two forests as a linked system offers increased flexibility for harvesting to help maintain sufficient mature, seed-bearing habitat for a viable red squirrel population.

The results from the model study have been incorporated into the proposed forest design plans for the Kidland and Uswayford region (under the Forestry Commission Cheviot Forest Plan proposal; pers. comm.). The revised plan is currently going through an approval procedure by the Forestry Commission and recommends a combination of forest design scenarios C and D for the harvesting and replanting strategy for these forests. Moreover, model findings highlighted the importance of a dispersal corridor between the two forests. Increasing the habitat linkage between the forests could in the long term help connectivity and provide a permanent corridor between the forests (but this is out with the scope of the Forestry Commission’s proposals). In general, the processes followed in this study have been an exemplar for how academic research can have a direct input to land management on the ground that helps managers objectively balance the differing pressures of multipurpose forestry.

Acknowledgements

AW, MB and PL are supported in part by a NERC Innovations grant NE/M021319/1. We are grateful for helpful suggestions from two anonymous referees.

Literature cited

Anonymous, 2012. Managing forests as red squirrel strongholds. Forestry Commission Practice Note 102: 1-16.

Bengtsson, J., Nilsson, S. G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132: 39-50.

Bosch, S., Lurz,, P. W. W. (2012). Eurasian Red Squirrel. Westarp Wissenschaften Verlagsgesellschaft mbH. Germany.

Brown, A., Webber, J., 2008. Red band needle blight of conifers in Britain. Forestry Commission Research Note 2: 1-8.

Carter, N., Levin, S., Barlow, A., Grimm, V. 2015. Modeling tiger population and territory dynamics using an agent-based approach. Ecological Modelling 312: 347-362.

DEFRA, 2011. Biodiversity 2020: A strategy for England's wildlife and ecosystem services: see www.defra.gov.uk.

Flaherty, S., Patenaude, G., Close, A., Lurz, P. W. W., 2012. The impact of forest stand structure on red squirrel habitat use. Forestry 85: 437-444.

Filyushkina, A., Strange, N., Lof, M., Ezebilo, E. E., Boman, M., 2016. Non-market forest ecosystem services and decision support in Nordic countries. Scandinavian Journal of Forest Research 31: 99-110.

Gurnell, J., Wauters, L. A., Lurz, P. W. W., Tosi, G., 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. Journal of Animal Ecology 73: 26-35.

Gurnell, J., Lurz, P. W. W., Bertoldi, W., 2014. The changing patterns in the distribution of red and grey squirrels in the North of England and Scotland between 1991 and 2010 based on volunteer surveys. Hystrix 25: 83-89.

Hansen, A. J., Spies, T. A., Swanson, F. J., Ohmann, J. L. Conserving Biodiversity in Managed Forests. BioScience 41: 382-392.

Holm J., 1991. The ecology of red squirrels (*Sciurus vulgaris*) in deciduous woodland. Ph.D. Thesis, University of London, UK.

Heikkinen, R. K., Pöyry, J., Virkkala, R., Bocedi, G., Kuussaari, M., Schweiger, O., Settele, J., Travis, J. M. J., 2015. Modelling potential success of conservation translocations of a specialist grassland butterfly. Biological Conservation 192: 200-206.

Kline, J. D., Moses, A., Burcsu, T., 2010. Anticipating forest and range land development in Central Oregon (USA) for landscape analysis, with an example application involving mule deer. Environmental Management 45: 974-984.

Lindenmayer, D. B., Margules, C. F., Botkin, D. B., 1998. Indicators of biodiversity for ecologically sustainable forest management. Conservation Biology 14: 941-950.

Lurz, P. W. W. 2015. Kidland and Uswayford Squirrel Monitoring 2015. Report to Forestry Commission, Kielder Forest District, Contract No. P255613, pp. 31

Lurz, P.W.W., Garson, P.J., Rushton, S.P., 1995. The ecology of squirrels in spruce dominated plantations: implications for management. Forest Ecology and Management 79: 79-90.

Lurz, P.W.W., Garson, P.J., Wauters, L., 1997. Effect of temporal and spatial variation in habitat quality on red squirrel, *Sciurus vulgaris*, dispersal behaviour. Animal Behaviour 54: 427-435.

Lurz, P.W.W., Garson P.J., Ogilvie J.F., 1998. Conifer species mixtures, cone crops and red squirrel conservation. Forestry 71: 67-71.

Lurz, P.W.W., Garson, P.J., Wauters, L., 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels, *Sciurus vulgaris* L. Journal of Zoology, London 251: 167-178.

Lurz, P.W.W., Rushton, S.P., Wauters, L.A., Bertolino, S., Currado, I., Mazzoglio, P., Shirley, M.D.F., 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. Landscape Ecology 16: 407-420.

Lurz, P. W. W., Geddes, N., Lloyd, A. J., Shirley, M. D. F., Burlton, B., Rushton, S. P., 2003. Planning red squirrel conservation areas: using spatially explicit population dynamics models to predict the impact of felling and forest design plans. Forestry 76: 95-108.

Lurz, P. W. W., Gurnell, J., Magris, L., 2005. *Sciurus vulgaris*. Mammalian Species 769: 1-10.

Lurz, P. W. W., Koprowski, J. L., Wood, D. J. A., 2008. The use of GIS and modelling approaches in squirrel population management and conservation: a review. Current Science 95: 918-922.

Macpherson, M.F., Davidson, R. S., Duncan, D. B., Lurz, P. W., Jarrott, A., White, A. 2015. Incorporating habitat distribution in wildlife disease models: conservation implications for the threat of squirrelpox on the Isle of Arran. Anim. Conserv. doi: 10.1111/acv.12219

Magris L., 1998. The ecology and conservation of the red squirrel (*Sciurus vulgaris*) on Jersey C.I.. Ph.D. Thesis, Queen Mary & Westfield College, University of London, UK.

Mikoláš, M., Svitok, M., Tejkal, M., Leitão, P. J., Morrissey, R C., Svoboda, M., Seedre, M., Fontaine, J. B., 2015. Evaluating forest management intensity on an umbrella species: Capercaillie persistence in central Europe. Forest Ecology and Management 354: 26–34

Ratcliffe, P. R., Petty, S. J., 1986. The management of commercial forests for wildlife. In: Trees and Wildlife in the Scottish Uplands. D. Jenkins. eds. Lavenham Press Ltd, Lavenham, Suffolk.

Shuttleworth, C. M., Lurz, P. W. W., Geddes, N., 2012. Integrating red squirrel habitat requirements with the management of pathogenic tree disease in commercial forests in the UK. Forest Ecology and Management 279: 167-175.

Parrott. D., Quy, R., K. Van Driel, Lurz, P. W. W., Gurnell, J., Aebischwer, N., Reynolds, J., 2009. Review of red squirrel conservation activity in northern England. Natural England, UK, Contract No. 08/09/N/004.

Pepper, H., Patterson, G., 1998. Red Squirrel Conservation. Forestry Commission Practice Note 5: 1-8.

Ray, D., 2008. Impacts of climate change on forestry in Scotland - a synopsis of spatial modelling research. Forestry Commission Research Note 101: 1-8.

Ray, D., Morison, J., Broadmeadow, M., 2010. Climate change: impacts and adaption in England's woodlands. Forestry Commission Research Note 201: 1-16.

Tompkins, D. M., White, A. R., Boots, M., 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. Ecology Letters 6: 189-196.

White, A., Lurz, P.W.W., 2014. A modelling assessment of control strategies to prevent/reduce Squirrelpox spread. Scottish Natural Heritage Commissioned Report No. 627.

White, A., Bell, S. S., Lurz, P. W. W., Boots, M., 2014. Conservation management within strongholds in the face of disease-mediated invasion: red and grey squirrels as a case study. Journal of Applied Ecology 51: 1631-1642.

White, A., Lurz, P.W.W., Bryce, J., Tonkin, M., Ramoo, K., Bamforth, L., Jarrott, A., Boots, M. 2016. Modelling disease spread in real landscapes: Squirrelpox spread in Southern Scotland as a case study. Hystrix. (In press).

Figure legends

Figure 1. (a) A photograph of Kidland forest highlighting how it is dominated by conifer. (b) The Forestry Commission relief map of Kidland and Uswayford forests and (c) the representation of compartments in the model with the Kidland compartments (blue), Uswayford (green) and Private (red).

Figure 2. Red squirrel carrying capacity estimates for Kidland, Uswayford and Tilhill in 2012. (a) The high estimate (Table 1) representing a good seed year and (b) the low estimate (Table 1) representing a poor seed year.

Figure 3. Changes in red squirrel carrying capacity using the high density estimates between 2012-2052 for scenario A and between 2012-2066 for scenarios B-D (summarised in Table 2). These scenarios were provided as an iterative process in response to model findings with scenario A provided on 24/2/14, scenario B on 14/10/14, scenario C on 17/11/14 and scenario D on 12/5/15.

Figure 4. (a) The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the '3 high, 1 low' carrying capacity scenario using the scenario A forest design plan for 2012-2052. The model was continued for an additional 20 years at the 2052 levels (highlighted by the dashed red line). (b) The same scenario as (a) with global dispersal (rather than the restriction of 1 km to dispersal).

Figure 5. The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the '3 high, 1 low' carrying capacity scenario. (a-c) represent scenario B, (d-f) scenario C and (g-i) scenario D (summarised in Table 2). The left column (a,d,g) represent realisations in which

the additional dispersal corridor between Tilhill and Uswayford is not included. The middle column (b,e,h) includes the additional dispersal corridor and assumes it can be utilized 30 years after planting. The right column (c,f,i) includes the additional dispersal corridor and assumes that it can be utilized 10 years after planting.

Figure 6. The percentage of realisations in which red squirrel populations persisted in Uswayford in 2052 for the four forest design scenarios (summarised in Table 2) when there is no dispersal corridor (left) and when the corridor is planted in the compartment shown in Figure S9 and has a 30 year growth time before it can be used (middle) or a 10 year growth time (right).

Table Legends

Table 1: Density estimates for red squirrels in the different tree species classes present in Kidland and Uswayford forest. The data was derived from the following references: Holm (1991); Magris (1998); Lurz et al. (1995, 1998); Bosch & Lurz (2012); White et al. (2014).

Table 2: A summary of the four different forest design plans (scenarios) created by the Forestry Commission.

Table 3: Possible events and their outcomes in a particular compartment *i*, with dispersal occurring to compartment *j*. The rates from Equation (1) are turned into probabilities by dividing by $R = \sum[\text{rates}]$ (the sum of the terms in square brackets summed over all compartments).

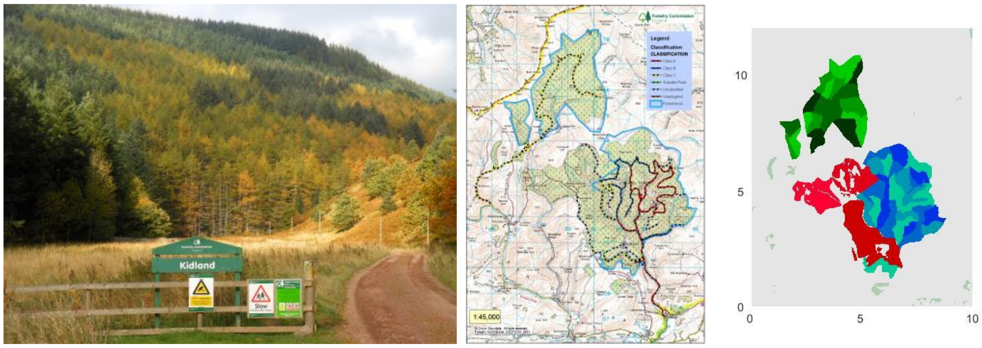

Figure 1. (a) A photograph of Kidland forest highlighting how it is dominated by conifer. (b) The Forestry Commission relief map of Kidland and Uswayford forests and (c) the representation of compartments in the model with the Kidland compartments (blue), Uswayford (green) and Private (red).

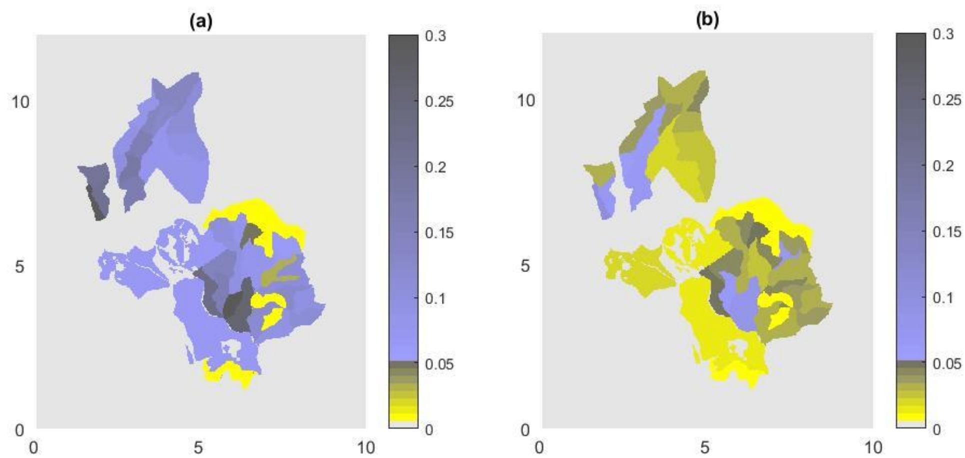

Figure 2. Red squirrel carrying capacity estimates for Kidland, Uswayford and Tilhill in 2012. (a) The high estimate (Table 1) representing a good seed year and (b) the low estimate (Table 1) representing a poor seed year.

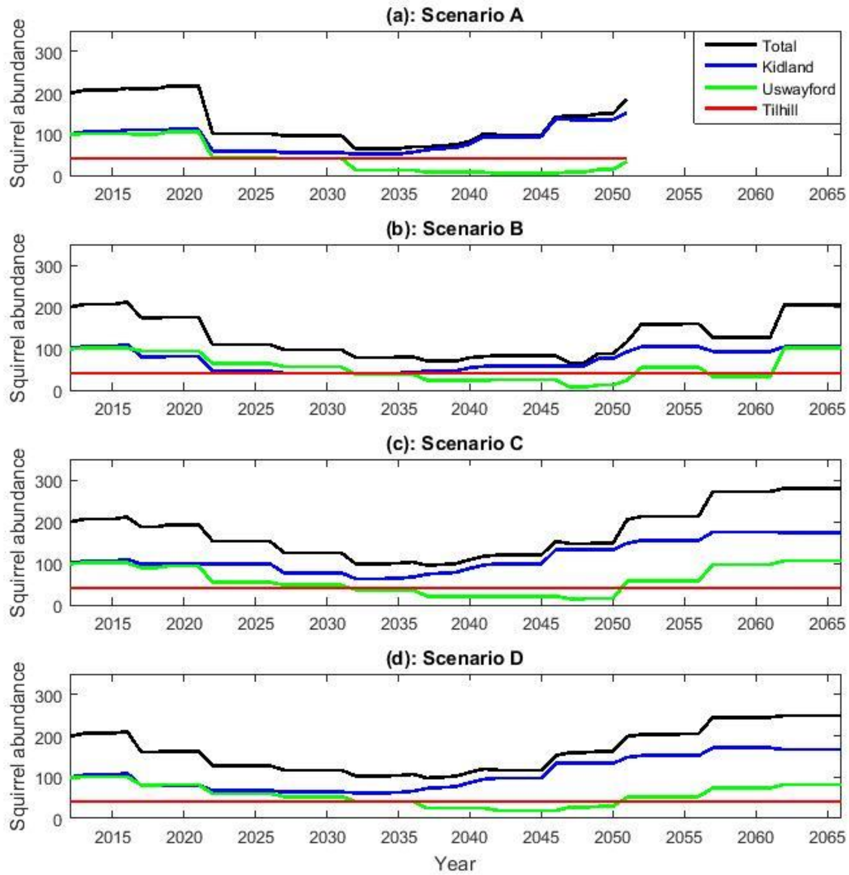

Figure 3. Changes in red squirrel carrying capacity using the high density estimates between 2012-2052 for scenario A and between 2012-2066 for scenarios B-D (summarised in Table 2). These scenarios were provided as an iterative process in response to model findings with scenario A provided on 24/2/14, scenario B on 14/10/14, scenario C on 17/11/14 and scenario D on 12/5/15.

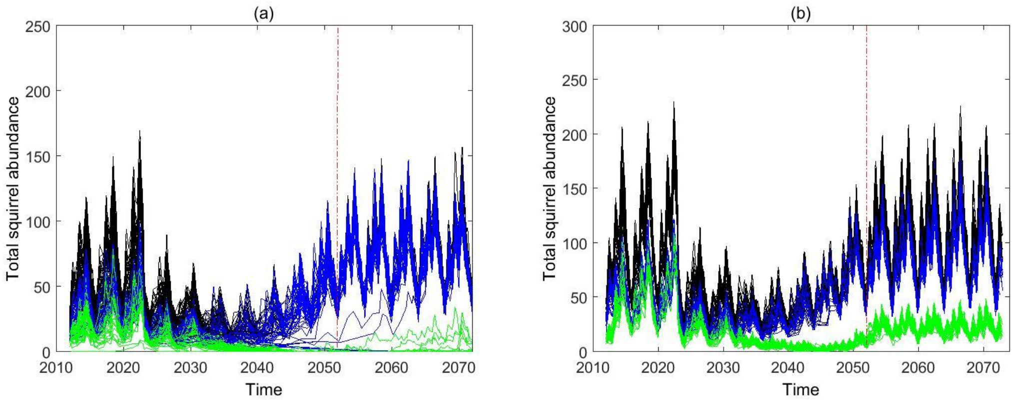

Figure 4. (a) The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the '3 high, 1 low' carrying capacity scenario using the scenario A forest design plan for 2012-2052. The model was continued for an additional 20 years at the 2052 levels (highlighted by the dashed red line). (b) The same scenario as (a) with global dispersal (rather than the restriction of 1km to dispersal).

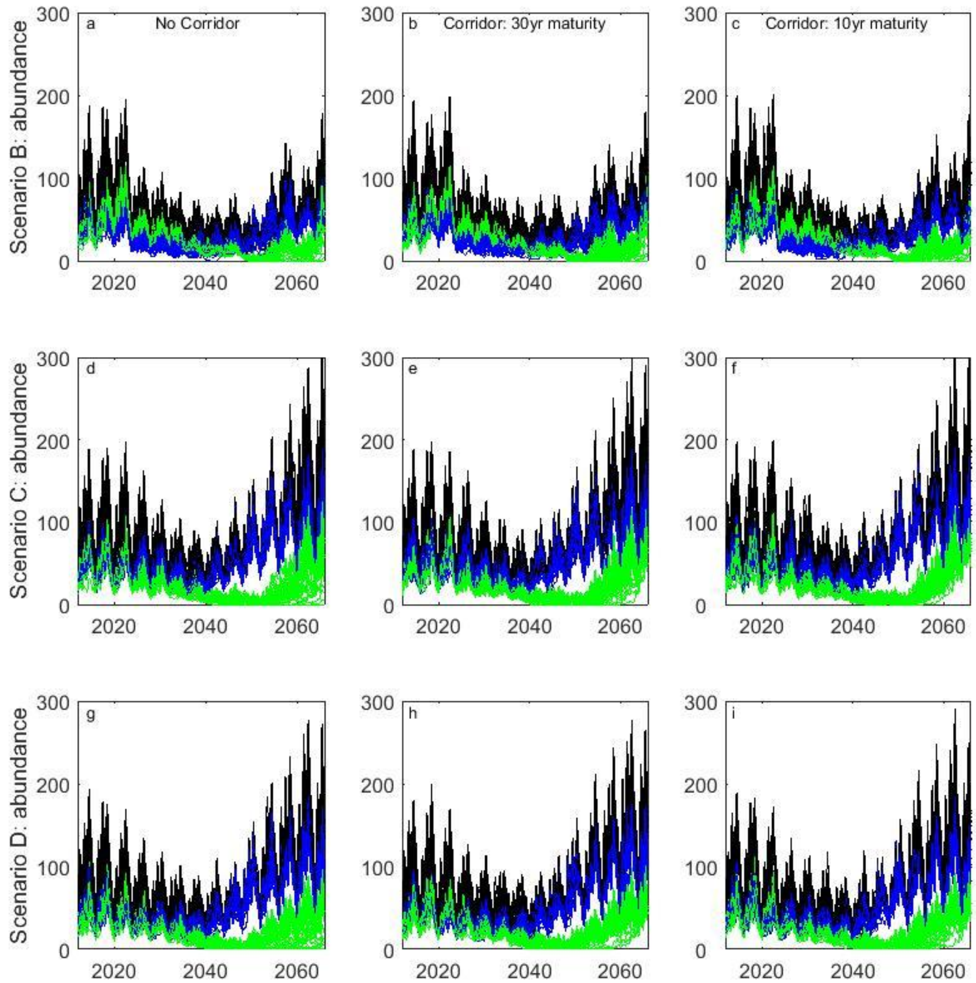

Figure 5. The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the '3 high, 1 low' carrying capacity scenario. (a-c) represent scenario B, (d-f) scenario C and (g-i) scenario D (summarised in Table 2). The left column (a,d,g) represent realisations in which the additional dispersal corridor between Tilhill and Uswayford is not included. The middle column (b,e,h) includes the additional dispersal corridor and assumes it can be utilized 30 years after planting. The right column (c,f,i) includes the additional dispersal corridor and assumes that it can be utilized 10 years after planting.

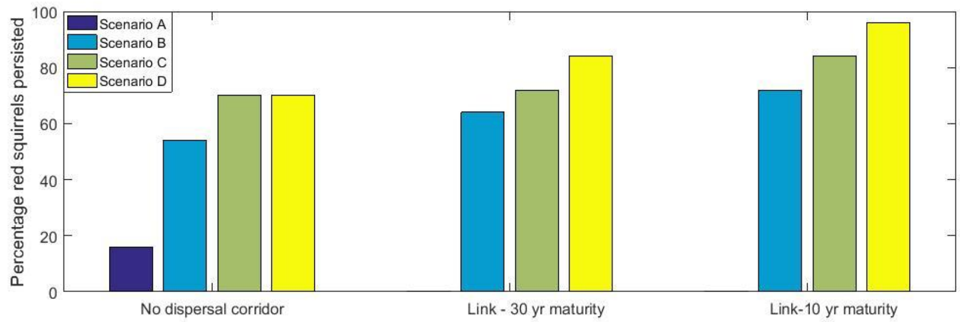

Figure 6. The percentage of realisations in which red squirrel populations persisted in Uswayford in 2052 for the four forest design scenarios (summarised in Table 2) when there is no dispersal corridor (left) and when the corridor is planted in the compartment shown in Figure S9 and has a 30 year growth time before it can be used (middle) or a 10 year growth time (right).